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Research Article

Even the losers: five-year distribution dynamics of alien plant species in South African savanna

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Abstract

We studied the short-term dynamics of the occurrence of alien plant species in a South African savanna. Within the MOSAIK (Monitoring Savanna Biodiversity in the Kruger National Park) project, plant species were recorded in a representative set of 60 plots, 50 m × 50 m in size, across the entire KNP in 2019–2020, distributed to cover a range of savanna habitats, i.e. perennial rivers, seasonal rivers and dry crests. The sampling focusing on alien plants was carried out in the same plots in 2024 and the changes in distribution patterns that occurred over the 4–5 years since the first sampling were assessed. In the first sampling period, 23 alien species were recorded and, in the second sampling, 20 were recorded; this gives a total of 25 alien species over the whole period of 2019–2024. In the recent survey, *Alternanthera pungens*, *Conyza bonariensis*, *Gomphrena celosioides*, *Bidens biternata* and *Achyranthes aspera* were most widespread, present in at least 10 plots. Using log-linear models, we showed that the total number of alien species records in plots did not significantly differ between the two sampling periods, indicating the absence of trends in species richness for the alien flora of KNP. There was a highly significant effect of habitat, with sites at perennial rivers harbouring more alien species than those at seasonal rivers and on crests. We also found a marginally significant interaction of habitat and sampling period, reflecting that the dry crests currently harbour fewer aliens than in 2019–2020. The frequency of some of the most invasive KNP species, such as *Parthenium hysterophorus*, *Xanthium strumarium* and *Opuntia stricta*, remained basically the same. However, *Conyza bonariensis* is an alien species that was quite rare in studied plots in 2019–2024, but its presence dramatically increased and it became widespread and locally abundant beyond the surveyed plots in some parts of KNP. Although not too successful until a few years ago, this species represents a future plant invasion threat in KNP.

Key words: Africa, dry savanna, longitudinal data, non-native species, plant invasions, riverine habitats

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Introduction

Plant invasions are amongst the most significant threats to global biodiversity and protected areas are no exception (Foxcroft et al. 2013, 2017; Pyšek et al. 2020b; IPBES 2023). Even though biological invasions affect biota in protected areas worldwide (e.g. Goodman 2003; Pauchard and Alaback 2004; Padmanaba et al. 2017; Pyšek et al. 2020b), a concern that dates back to the 1860s (Foxcroft et al. 2017), very few protected areas have good baseline information and only a handful

of those that are well-studied have robust invasive alien species lists available (see IPBES 2023 and examples referred therein).

Although studies reported from several parts of the world that some protected areas act as a barrier against the spread of alien plant species (Pyšek et al. 2003; Foxcroft et al. 2011; Gallardo et al. 2017), most are vulnerable to invasions and only rarely are they entirely free of alien species (Foxcroft et al. 2017; Moodley et al. 2020). The presence of alien invaders brings about a variety of impacts on species, communities and protected ecosystem that include the alteration of habitats, ecosystem regime shifts and losses to native species abundance, diversity and richness (Foxcroft et al. 2013; Hulme et al. 2014; Pyšek et al. 2020b; Novoa et al. 2021). Invasive plants are also regarded as a significant threat by the managers of protected areas (Pyšek et al. 2013; Shackleton et al. 2020). Of various taxonomic groups of invasive organisms, plants posed the greatest continued threat in a study analysing trends over ~ 30 years from the 1980s to the present, where their species numbers increased in 31% of the protected areas (Shackleton et al. 2020).

Most data on the occurrence of alien and invasive plants recorded in the field are collected in a particular place only once. Yet, longitudinal field data proved most helpful in providing information on invasion dynamics. If such data, based on permanent plots and repeated sampling, exist, they are primarily used to determine the spread of the populations of invasive species (Müllerová et al. 2005) and monitor changes in their impact (Yurkonis and Meiners 2004; Jäger et al. 2009; Dostál et al. 2013). Longitudinal data are, however, also crucial for assessing the dynamics of alien species participation in plant communities over time at a fine-grain scale (Miller et al. 2021; Kermavnar and Kutnar 2024) and identifying factors driving these dynamics (Staudhammer et al. 2015).

In the Kruger National Park, South Africa, a significant threat from alien plant invasions to the savanna ecosystem is associated with rivers that act as the most efficient pathways for propagules from adjacent areas (Pyšek et al. 2020a; Foxcroft et al. 2023; Hejda et al. 2023). Rivers and associated riparian habitats have been repeatedly demonstrated to harbour disproportionally more alien species, including some remarkable invaders, because of strong propagule pressure, supply of nutrients and provision of safe sites for germination and establishment (Pyšek and Prach 1993; Planty-Tabacchi et al. 1996; Foxcroft et al. 2007; Richardson et al. 2007; Pyšek et al. 2010).

In other systems, alien invaders that were confined to riverbanks and riparian areas for a long time have started to spread to surrounding environments, such as *Impatiens glandulifera* in central Europe (Čuda et al. 2017, 2020). However, the data collection in KNP has focused so far on alien species hotspots in human-disturbed habitats, such as tourist camps and other infrastructure or riverbeds. Systematically investigating distributions of alien plants across the entire park would allow us to assess how successfully they persist in various habitats and whether spreading from riverbeds also happens in KNP. Still, such information was missing until a few years ago (Pyšek et al. 2020a). To close this gap, an effort was made within the MOSAIK (Monitoring Savanna Biodiversity in the Kruger National Park) project, which is focused on studying biodiversity across the entire KNP (Delabye et al. 2022; Hejda et al. 2022; Čuda et al. 2024). There, we assessed to what extent alien plants are confined to rivers as the primary introduction pathway and dispersal vector versus how commonly they occur in drier habitats away from rivers (Pyšek et al. 2020a).

Here, we explore the fine-scale dynamics of alien species occurrences over 4–5 years in the South African savanna, based on repeated sampling of the same plots. This research has been motivated by the fact that it is unknown: (i) how great the fluctuation in their presence is across various habitats, i.e. how much their contribution to overall plant species richness is changing over time, (ii) what is the effect of habitat (i.e. by perennial rivers, seasonal rivers and on dry crest) on these dynamics and on alien species persistence and (iii) how stable are the populations of individual species. At the time of the first sampling (2019–2020), the covers of alien species in plant communities were generally low (Pyšek et al. 2020a), which is in sharp contrast to riverbeds in KNP where the invasions are large-scale, stable and persistent (Hejda et al. 2022, 2023). Thus, it is legitimate to ask how persistent are these small populations of alien species beyond riverbeds, how much they fluctuate or shift across savanna and whether some of these apparent "losers" have the potential to generate future threats to savanna biodiversity.

Methods

Study area

Kruger National Park (KNP), established in 1898, is the largest game reserve in South Africa and one of the oldest national parks in the world (Carruthers 1995). It is located in the north-eastern part of the country, covering an area of 19,169 km^2 and stretching ~ 450 km north-south and 84 km east-west. The majority of KNP has a subtropical climate, with the Tropic of Capricorn crossing the Park in the north and several perennial rivers flow through the Park, mainly in a west-east direction (i.e. Sabie, Olifants, Crocodile, Letaba, Shingwedzi, Luvuvhu and Limpopo; Fig. 1). The Park has diverse geological conditions (granitoid bedrock in the western vs. volcanic, mainly basalt and gabbro, in the eastern part), altitude (140–780 m a.s.l.), climate (450–750 mm of annual precipitation) and vegetation (dominant woody species, proportional representation of woody cover vs. open grassland; MacFadyen et al. 2016).

A recent update of the alien flora of KNP focused on species that occur in natural areas in KNP (i.e. beyond tourist camps and other infrastructure) and, thus, represent a potential threat to the diversity of native species. This work identified 146 alien plant taxa, of which 30 are casuals, 58 are naturalised, 21 have become invasive (in the sense of Richardson et al. 2000, i.e. rapidly spreading across the Park) and 37 with unresolved status (see Foxcroft et al. 2023, also for details on the assessment of invasion status of particular taxa). Twelve of the invasive species in KNP are globally widespread and five (i.e. *Pontederia crassipes*, *Lantana camara*, *Opuntia stricta*, *Chromolaena odorata* and *Mimosa pigra*) are listed amongst 100 of the world's worst invasive alien species (Invasive Species Specialist Group 2013).

Data collection

The data were collected for the MOSAIK project (Monitoring Savanna Biodiversity in the Kruger National Park), whose primary objective was to sample plant and animal biodiversity in habitats across KNP (Delabye et al. 2022; Hejda et al. 2022; Čuda et al. 2024). To this purpose, we established triplets of 50 m × 50 m plots, each triplet including a site: (i) near a perennial river or another permanent

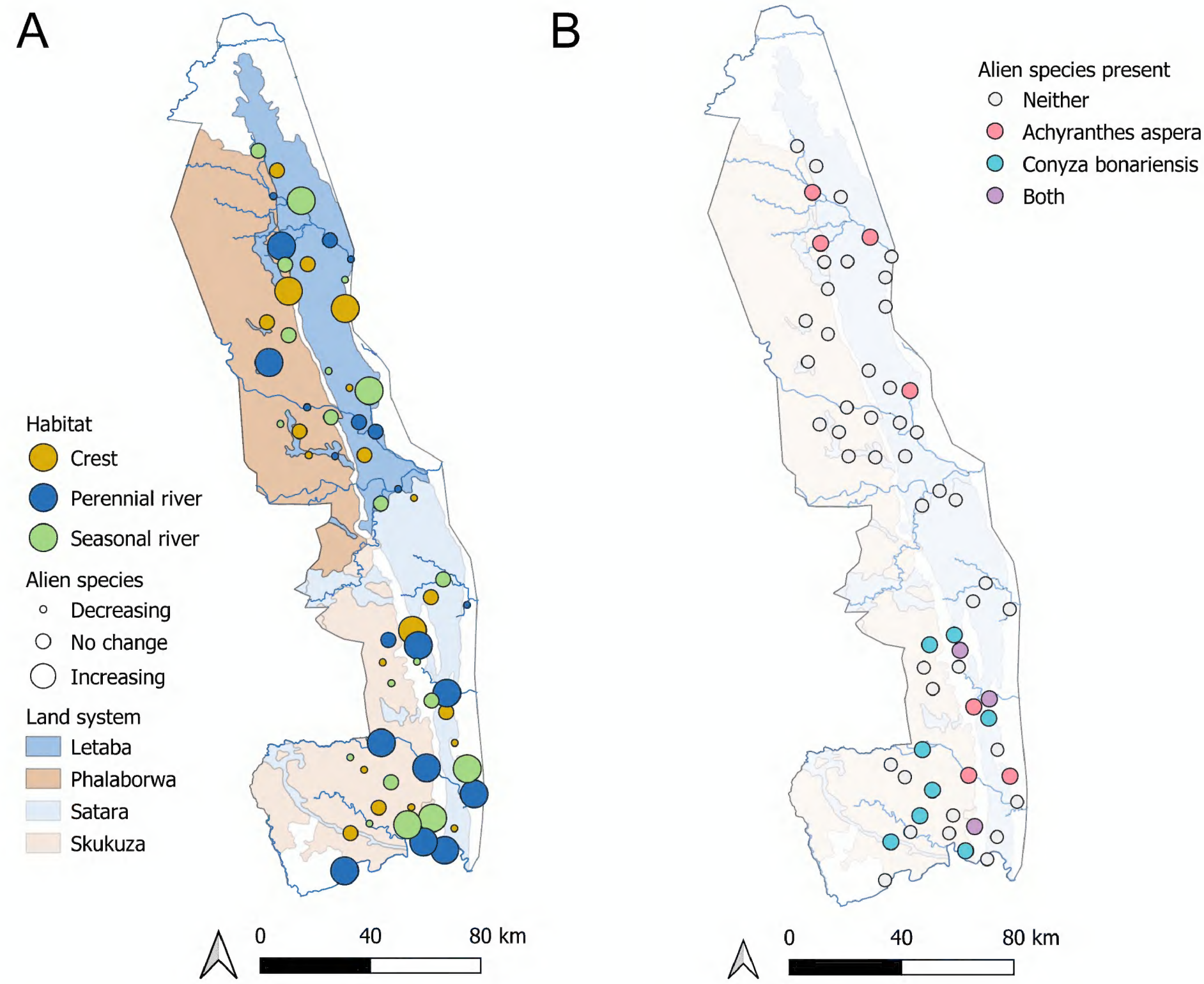

Figure 1. **A** The Kruger National Park with the location of the 60 sampled sites, separated according to habitat and distributed across the four land systems. The colour of the symbols refers to the habitat and its size indicates the change in the number of alien species recorded in a plot between the first (2019–2020) and second (2024) sampling **B** distribution of the two alien species that exhibited the most pronounced spread during the study period.

source of water such as a dam or pool (the criterion being water present all year round), (ii) near a seasonal river, defined as a river or stream where water is only present in the rainy season and (iii) on a dry crest at least 5 km from any source of water (Fig. 1). The plots within each triplet were selected to capture the different habitats in a similar landscape context within a reasonable distance of ~ 7–13 km amongst plots. There were 20 triplets distributed to cover the four land systems in KNP (defined based on the association between geology, terrain morphology, soils and woody vegetation; Venter 1990) with five triplets in each, giving a total of 60 plots (Fig. 1). Consequently, each of the three habitats was sampled with 20 plots and each of the two bedrock (granite, basalt) types with 30 plots.

During two rainy seasons, 16 January to 4 February 2019 and 17 January to 3 February 2020 (further termed 'first sampling'; see Hejda et al. 2022 for more details), all vascular plant species were recorded in each 2500 m^2 plot and their abundance estimated visually using the Braun-Blanquet cover-abundance seven-grade scale (Mueller-Dombois and Ellenberg 1974). From the data, we identified species that are alien to South Africa and considered introduced by humans to regions

outside their native range (see Pyšek et al. 2004; Essl et al. 2018 for definitions). To classify alien species as naturalised (forming self-sustainable populations in the wild) or invasive (a subgroup of naturalised species rapidly spreading in the invaded area), we followed the definition proposed by Richardson et al. (2000) and Blackburn et al. (2011). This classification of species status was based on a recent catalogue of alien plants in KNP (Foxcroft et al. 2023).

On 9–21 March 2024 (further termed 'second sampling'), the same plots were surveyed with a focus on all alien species, not only those recorded in 2019–2020, but also those that arrived since the first sampling. Given the sampling dates in the first period, 33 plots were surveyed after five years and the remaining 27 after four years (see Hejda et al. 2022). The covers of all alien species recorded were very low and did not exceed degree 1 of the Braun-Blanquet scale (Mueller-Dombois and Ellenberg 1974), which corresponds to 1–5% of the plot cover; the covers of species that qualified for this assessment mostly approached even the lower threshold of this degree percentage value. Therefore, the analyses focused on species' presence and absence in the plots rather than their abundance proxied by cover.

Statistical analysis

The differences in the numbers of aliens (frequencies of occurrences in the sampled plots) were tested by generalised mixed-effect models (GLMM), with the triplet identity set as a random effect and the three plots within a triplet considered as pseudoreplicates: m1 <- glmer(number of alien species ~ sampling time*habitat type +(1|triplet), family=poisson). We also ran a GLMM model that included "land systems" and "triplets" (nested in land systems) as random effects: glmer(number of species ~ sampling time*habitat +(1|landsytem)+(1|triplet),family=poisson). This model provided results very similar to the GLMM with only "triplets", which yielded lower AIC, indicating better parsimony (424.5 compared to 425.9 of the model that included land systems). Therefore, we only present the results of the GLMM model with triplets. The GLMM models were created using the package "lme4" of the R statistical software (Bates et al. 2015). The significance of individual terms (sampling time: first sampling in 2019–2020 vs. second in 2024; habitat type: perennial river, seasonal river, crest; sampling time:habitat type interaction) were tested by likelihood ratio tests, where non-significant terms ($p > 0.05$) were deleted. The differences between individual levels of habitat type were tested by the Tukey post-hoc method, using the R package "emmeans" (Lenth 2024). The accuracy of the parsimonious model was checked by inspecting the normality of residuals using the Shapiro-Wilk normality tests.

The numbers of persisting, newly emerging and disappearing species (in comparison with the first sampling) in individual habitats (perennial rivers, seasonal rivers, crests) were tested using log-linear models of the R software. Similar to the GLMM models with the number of alien plant species as a response variable, the species persistence category (persisting, newly emerging, disappearing) and habitat were predictors. The significance of individual terms was tested by likelihood ratio tests and the differences between the levels of factor predictor (persistence category: persisting species, newly-emerging species, disappearing species; habitat type: perennial rivers, seasonal rivers, crests) were tested by Tukey post-hoc comparisons using the package "emmeans". The differences in the frequencies of occurrences of individual species between the two samplings were tested using chi-square tests, by comparing

the total numbers of plots, in which the species was recorded in 2019–2020 versus in 2024, with the aim to find out which alien species decreased or increased their total frequency of occurrence, regardless of the three different habitats.

A direct gradient analysis (CCA) was used to test the overall differences in plant species composition between the first and second sampling. A split-plot sampling scheme was used to reflect the hierarchical arrangement of plots in triplets. The triplets were set as whole-plots and the plots within the triplets were the split-plots. Both whole-plots and split-plots were permuted freely, with 499 permutations.

Results

Numbers and frequencies of alien species

In the first sampling period, 23 alien species were recorded and, in the second sampling, there were 20. In total, 25 alien species were recorded over the five-year study period. Some species data presented here differ slightly from those shown in the previous paper (Pyšek et al. 2020a). The reasons for this discrepancy are: (i) revisiting the native status in uncertain cases (e.g. *Boerhavia diffusa*, *Mollugo nudicaulis* and *Schkuhria pinnata* are now considered alien, while *Litogyne gariepina* and *Melanthera scandens* were reconsidered as native), (ii) re-identification of herbarium specimens of rare species, which yielded alien *Amaranthus standleyanus*, *Conyza bonariensis* and *Sesbania bispinosa* that are now included in the list (Table 1).

The frequencies of alien species, expressed as the total number of species-plot records were 118 in 2019–2020 and 122 in 2024 (Table 1) and differed significantly amongst individual habitats ($\chi^2 = 97.929$, DF = 2, $p < 0.001$). The Tukey tests showed that perennial rivers harboured more aliens than either seasonal rivers or crests (both $p < 0.001$), but the difference between seasonal rivers and crests was not significant. Further, there was a marginally significant interaction between the sampling time and habitat ($\chi^2 = 4.744$, DF = 2, $p = 0.093$), indicating that the distribution of aliens in individual habitats (perennial rivers, seasonal rivers, crests) differed between the first and second sampling. In particular, the crests exhibited even fewer species-plot records in 2024 than in the first sampling in 2019–2020 (Table 1).

Persistence of alien species

The distribution of species amongst the persistence categories (persisting, newly emerging, disappearing) differed ($\chi^2 = 27.467$, DF = 2, $p < 0.001$; Table 2). There were fewer persisting species than newly-emerging alien species and disappearing alien species (both $p < 0.001$ in Tukey post-hoc comparisons). There was also a significant interaction between the habitat type and persistence category ($\chi^2 = 15.486$, DF = 4, $p = 0.004$), indicating that the frequency of species in persistence categories differed according to habitats. This is most likely due to lower persistence of aliens at seasonal rivers and crests (Table 2).

The persistence, emergence and disappearance of individual species are presented in Table 1. The percentage persistence (defined as % of plots in which a taxon was present in both the first and second samplings; Table 1) ranged from very high values (*Acanthospermum hispidum* 80%, *Althernanthera pungens* 75%, *Gomphrena celosioides* 57%) to very low (*Mollugo nudicaulis* 7%, *Bidens bipinnata* 17%) to complete disappearance (e.g. *Conyza bonariensis*, *Achyranthes aspera*). In the latter

Table 1. The occurrence of alien species in the Kruger National Park, recorded over two time periods. Species presented in bold significantly differed in their frequency in 60 plots between the two periods and the statistics of the difference are shown. Species marked with an asterisk are not listed in Pyšek et al. (2020) (although they were recorded in 2019–2020), because of reconsideration of their status or re-determination of the botanical material (see text for details). Life history: a – annual herb, p – perennial herb, ss – subshrub, s – shrub. The last column indicates the number of plots in which the taxon persisted (P), newly emerged (E) and from which it disappeared (D) between the first and second sampling. Status in the recent catalogue of alien plants in KNP (Foxcroft et al. 2023) is (St column): n = naturalised, i = invasive, u = unknown, – = not listed.

Taxon	St	Family	Life history	Origin	2019–2020	2024	χ^2	p-value	P-E-D
Acanthospermum hispidum	n	Asteraceae	a	tropical America	5	9	–	–	4-5-1
Achyranthes aspera	n	Amaranthaceae	p	Mediterranean	2	10	6.23	0.013	0-10-2
Alternanthera pungens	n	Amaranthaceae	p	tropical America	8	13	–	–	6-7-2
*Amaranthus standleyanus**	–	Amaranthaceae	a	S America	1	0	–	–	0-0-1
Argemone ochroleuca	n	Papaveraceae	a	N America	1	0	–	–	0-0-1
Bidens bipinnata	n	Asteraceae	a	Asia, N America	6	9	–	–	1-8-5
Bidens biternata	n	Asteraceae	a	E Asia (Himalayas)	10	10	–	–	3-7-7
*Boerhavia diffusa**	u	Nyctaginaceae	a, p	tropics and subtropics	8	7	–	–	2-5-6
Chenopodium album agg.	–	Amaranthaceae	a	Eurasia	1	0	–	–	0-0-1
Conyza bonariensis*	n	Asteraceae	a	C and S America	2	11	6.23	0.013	0-11-2
Datura inoxia	i	Solanaceae	a, p, ss	N America	1	0	–	–	0-0-1
Gomphrena celosioides	n	Amaranthaceae	a, p	S tropical America	7	11	–	–	4-7-3
Malvastrum coromandelianum	n	Malvaceae	a, p, ss	tropical to subtropical America	10	9	–	–	4-5-6
Mollugo nudicaulis*	–	Molluginaceae	a	unclear	14	3	8.90	0.003	1-2-13
Opuntia ficus-indica	n	Cactaceae	p	C America	0	2	–	–	0-2-0
Opuntia stricta	i	Cactaceae	p	N America	3	3	–	–	1-2-2
Parthenium hysterophorus	i	Asteraceae	a	N America	8	7	–	–	3-4-5
Portulaca oleracea	n	Portulacaceae	a	Eurasia	4	1	–	–	1-0-3
Senna septentrionalis	n	Fabaceae	s	C America	0	3	3.00	0.083	3-0-0
*Schkuhria pinnata**	u	Asteraceae	a	S America	9	7	–	–	4-3-5
*Sesbania bispinosa**	n	Fabaceae	a	tropical Asia and Africa	1	1	–	–	0-1-1
Tridax procumbens	n	Asteraceae	a, p	C America	11	2	6.23	0.013	0-2-11
Verbesina encelioides	n	Asteraceae	a	S America	1	0	–	–	0-0-1
Xanthium strumarium	i	Asteraceae	a	N America	3	3	–	–	0-3-3
Zinnia peruviana	i	Asteraceae	a	America	2	1	–	–	1-0-1
Number of species					23	20			
Sum of occurrences									
Total					118	122			
Perennial rivers					70	84			
Seasonal rivers					25	26			
Crests					23	12			

Table 2. Persistence of alien species in particular habitats between first (2019–2020) and second (2024) sampling. The numbers are species-plot records of all aliens in each category.

Persistence category	Perennial	Seasonal	Crest	Total
Persisting	29	4	2	35
Newly emerging	55	22	10	87
Disappearing	41	21	21	83

two species, the disappearance from a few plots was compensated by new emergence in many plots at the second sampling. The percentage emergence (% of the total number plots in which the species was present only at the second sampling; Table 1) ranged from 43% to 100%, indicating that, for most species, their current frequency is mainly due to new records (Table 1).

Changes in frequencies of individual alien species

Of the 26 species recorded in both periods, only six (23.1%) have significantly changed their frequency (Table 1). Three species that increased are *Achyranthes aspera*, *Conyza bonariensis* (both from 3% to 18% of plots) and *Senna septentrionalis* (not present in 2019–2024, in 3% of plots in 2024), while *Mollugo nudicaulis* (from 26% to 5% of plots) and *Tridax procumbens* (from 18% to 3%) decreased (Fig. 2). The changes in frequencies of these species within habitats are shown in Suppl. material 1.

The direct gradient analysis (CCA) with binary data on the presence/absence of individual alien species as responses revealed significant compositional differences between the first sampling and second sampling ($p = 0.004$) because, as described above, some aliens considerably increased their frequencies, while others declined (Suppl. material 2).

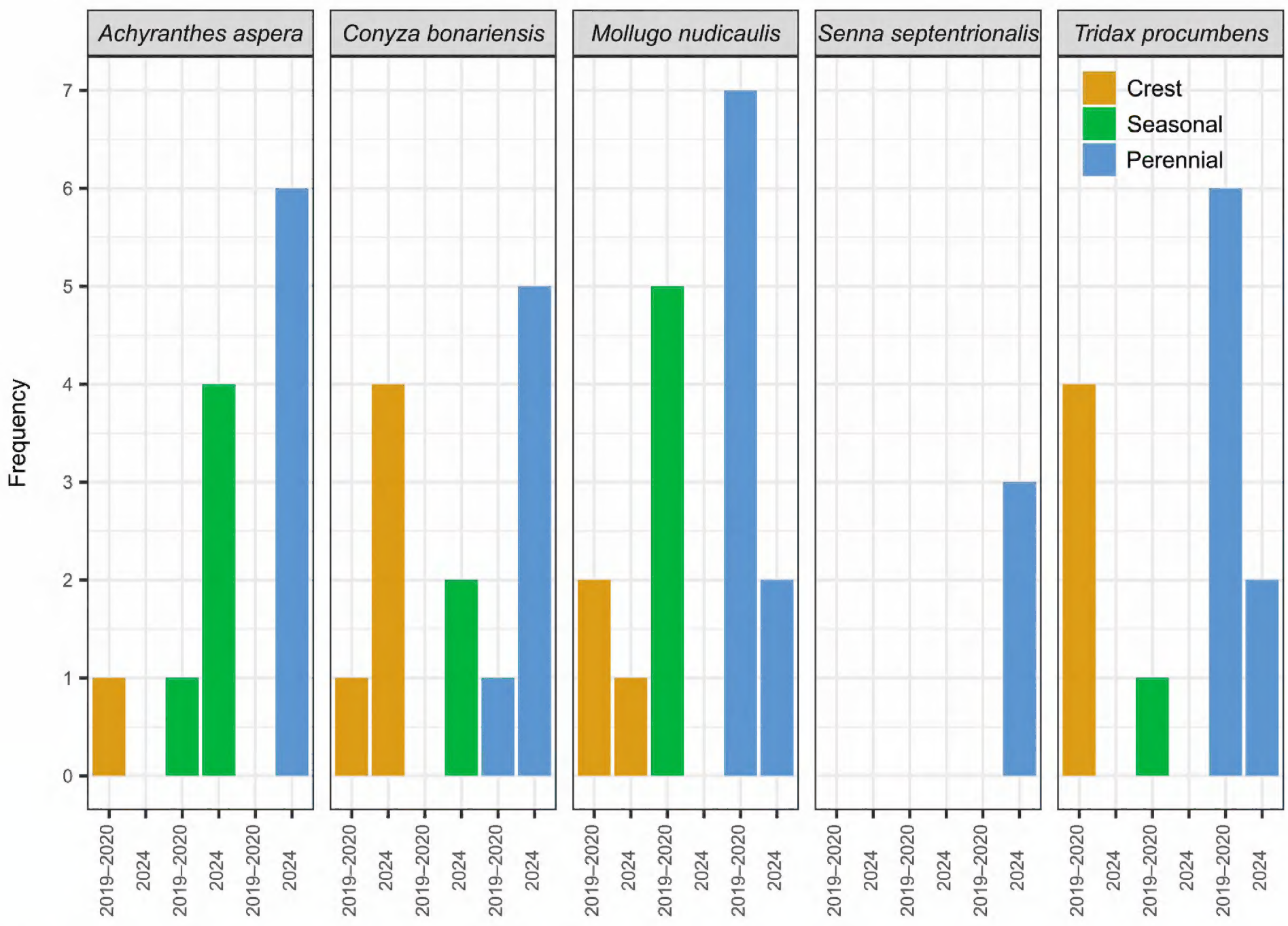

Figure 2. Changes in frequencies of species between the first (2019–2020) and second (2024) sampling at perennial rivers, seasonal rivers and crests (for each habitat n = 20). Only species whose frequencies changed significantly over the five years of study are shown (see Table 1).

Discussion

Stable alien flora composed of fluctuating species

Although we found differences in species composition of the alien flora in KNP as recorded in 2019–2020 vs. 2024, the total number of alien plant species has not changed over the 4–5-year period of the study. There was a decrease in the total number of aliens recorded across all plots, from 23 to 20, but this difference was not significant. However, individual alien species tend to fluctuate, as revealed by the low persistence of some species, along with the numbers of those newly emerging or disappearing. These data illustrate that low persistence in sites once colonised is not a constraint to successful invasion at the scale of the whole Park. Moreover, it needs to be emphasized that some globally noxious invaders continue to persist in KNP, such as *Parthenium hysterophorus* (Foxcroft et al. 2024) and *Opuntia stricta* (Novoa et al. 2021); the first species is listed amongst the invasive species of European Union concern (Brundu et al. 2022) and the second amongst IUCN 100 worst species (Invasive Species Specialist Group 2013).

Concerning individual species, *Achyranthes aspera*, *Conyza bonariensis* and *Senna septentrionalis* increased their frequency most remarkably; *A. aspera* invaded near perennial and seasonal rivers, *C. bonariensis* mainly near perennial rivers and on crests and *Senna septentrionalis* invaded near perennial rivers. The opposite trend, i.e. being markedly less frequent during recent sampling, was found for *Tridax procumbens*, especially near perennial rivers and on crests.

Determining native or invasive status and distinguishing morphologically similar plant species is a challenge for field-based research like that presented here. An example of the former would be *Achyranthes aspera*, which is considered native to many parts of northern, western and eastern Africa, but it is very likely alien to South Africa (van der Walt 2009, https://www.botany.cz). The situation is further complicated by the treatment of this species at the infraspecific level. In KNP, the *A. aspera* var. *sicula* is considered an alien taxon (van der Walt 2009). However, at the species level, *A. sicula* is sometimes referred to as a synonym of *A. aspera*. The genus *Boerhavia* is an example of the latter issue – *B. diffusa* is considered alien to the broader region around KNP (Pooley 1998), while *B. repens* is regarded as native (van der Walt 2009). However, it is very difficult to distinguish these two species in a sterile state. While we consider it fair to admit these uncertainties we encountered, we acknowledge that they do not affect the results reported here that focus on the overall pattern in species richness over time.

Comparison with the most recent catalogue of alien plants in KNP (Foxcroft et al. 2023) revealed that five species recorded in our plots are considered invasive at the whole-park scale, 14 are naturalised and two (*Boerhavia diffusa*, *Schkuhria pinnata*) are listed with unknown status (Table 1). Of the latter category, both species were relatively common in the study plots and their occurrence remained constant over time (seven plots, i.e. 12%) – this might be a reason to reconsider their status as naturalised. Three taxa (*Amaranthus standleyanus*, *Chenopodium album* agg. and *Conyza bonariensis*) represent additions to the alien flora of KNP. *Mollugo nudicaulis* is not listed as alien by Foxcroft et al. (2023), who considered it extralimital. The information on the origin of this species varies; in our treatment, we considered it alien, following the local flora of the Limpopo Valley (van der Walt 2009).

The role of habitat

The distribution of alien species in the three habitats studied, i.e. perennial rivers, seasonal rivers and crests, reveals a similar pattern as in 2019–2020, with perennial rivers showing higher numbers of aliens compared to either seasonal rivers or crests (Pyšek et al. 2020a). Interestingly, we found a marginally significant interaction between the effects of the sampling period and habitat, suggesting that the distribution of aliens in habitats between the two sampling dates differs. It appears that the crests have become even poorer in aliens since 2019–2020.

A similar result documenting the lower capacity of dry sites to harbour alien species (Rejmánek 1989; Milton and Dean 2010; Pyšek et al. 2017) is that the numbers of species that persisted in the same plot at crests from 2019–2020 to 2024 were lower than those of newly-recorded species and those that disappeared. Species persistence was higher near perennial rivers than near either seasonal rivers or on crests.

It is rather speculative to explain these trends, based on the relatively short time between the two samplings. One factor that may play a role is the warming climate that is generally unsuitable for plant invasion in arid areas (Pyšek et al. 2017) and, for KNP specifically, it has been shown that high temperatures constrain the plant species richness in general (Hejda et al. 2022).

Even the losers: rapidly emerging invasion threats

Despite relatively stable invasion-related characteristics of the whole flora across the habitats studied, the rapid spread observed for some species, namely *Conyza bonariensis* (Asteraceae), indicates that future invaders may suddenly recruit from relatively small and inconspicuous populations that were persisting in the landscape for a long time. *Conyza bonariensis* was first recorded in KNP in 1952 (Foxcroft et al. 2023), but remained rare for decades and, thus, was considered unsuccessful as an invader. Currently, this species has well-established populations in the southern part of the KNP (Fig. 1B), forming dominant stands in many places (Fig. 3). As one of a few spreading aliens, it is not restricted to river plots – 36% of its occurrences are on crests (Suppl. material 1). Its spread may become a serious conservation problem because crests often harbour rare species (Hejda et al. 2022). The rapid recent spread of this species is emphasised by it not being included amongst invasive taxa even in the most recent edition of the catalogue of alien plants in KNP (Foxcroft et al. 2023). Currently, its populations are naturalised in KNP and starting to spread. Therefore, it can already be considered invasive by standard ecological definitions (Richardson et al. 2000; Blackburn et al. 2011), but to confirm this status with certainty, a longer observation period is needed. Seeds of this species are easily dispersed by wind and *C. bonariensis* could, therefore, invade large areas of savanna in KNP at the expense of resident vegetation and native species. *Conyza bonariensis* is a common weed in dryland minimum tillage farming systems in Australia and the Mediterranean, with seeds germinating best from shallow burial and in lighter soils (Wu et al. 2007). Conditions in savannas are likely similar to those in minimum tillage fields, with *C. bonariensis* occupying patches of bare soil disturbed by large herbivores. The species was documented to be resistant to glyphosate in the Mediterranean, South America and South Africa (Dinelli et al. 2008), which makes it difficult to manage. The invasion potential of

Figure 3. *Conyza bonariensis* is an alien species that was quite rare in studied plots in 2019–2024, but its presence increased more than five times (2 vs. 11 records) and it has become widespread and locally abundant beyond the surveyed plots in some parts of KNP. The upper image shows a stand near the N'waswitsontso River, the bottom image a detail of the inflorescence.

C. bonariensis, a species originating from South America, is confirmed by its ranking amongst the naturalised alien species of the world, based on the analysis of the GloNAF database (van Kleunen et al. 2015, 2019). This species has been recorded as naturalised in 227 regions of the world (out of the 844 assessed), including 38 regions in Africa, which ranks it as the 31st most widely distributed alien naturalised species of the ~ 14,000 registered (Pyšek et al. 2017).

In general terms, extreme environments, such as arid ones, may harbour relatively few invasive species, but these are often strong invaders (e.g. Clarke et al. 2005; Kumar and Mathur 2014) and their impact on biodiversity can be severe because dry habitats often host rare species that are threatened by the invader (e.g. Gaertner et al. 2009; Fried et al. 2014).

Achyranthes aspera (Amaranthaceae) is not as widespread and dominant beyond the surveyed plots as *C. bonariensis*, but it is not restricted to a specific part of KNP (Fig. 1B). It is listed as naturalised in the recent catalogue of alien plants in KNP (Foxcroft et al. 2023). The fruit of this species has spiny bracts that adhere to animal skin and is thus effectively spread over a long distance (Bullock and Primack 1977). Spread by animals may be a reason for the strong affiliation of this species with rivers (91% of occurrences are along rivers; Suppl. material 1). Reported as naturalised from 160 regions of the world, 52 of which are located in Africa (Pyšek et al. 2017), this species is another candidate for a future problematic invader.

Longitudinal field data from permanent plots are the best way to precisely record changes in the performance and distribution of alien species, for which rapid dynamics are typical. The relatively short period assessed in the current paper indicates that changes in the performance of individual alien and invasive species may occur relatively quickly. To determine the consistency of observed trends and whether the increases or decreases of some species are just fluctuations over time, it is advisable to collect such data over a more extended observation period. More generally, alien species are linked to biodiversity change, but the extent to which they are associated with the reshaping of ecological communities is not well understood; repeated sampling of plots where alien plants were recorded in the past, such as the BioTime database (Dornelas et al. 2018; Knollová et al. 2024) has potential to provide insights into how alien species affect plant community dynamics. A study using data from repeated surveys found that, even in communities where alien species were typically rare, their presence was associated with an increase in the average rate of compositional change, mainly due to species replacement (Kortz et al. 2023).

Our paper shows that even small populations of alien species that fluctuate in their abundance and shift their distribution across savanna habitats may exhibit considerable dynamics over a short period of time and present threat to savanna biodiversity. These results can provide justification for managers in protected areas to argue for funding to repeatedly survey alien species, their distributions and impacts.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

PP initiated the idea, MH, JČ and PP collected the data, MH analysed the data, PP and MH wrote the first draft of the manuscript, JČ, KP and MH prepared the figures, all authors discussed the results, contributed to editing and writing.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

Number of records of species whose frequency has significantly changed between the first and second sampling, shown separately for particular habitats

Authors: Petr Pyšek, Jan Čuda, Llewellyn C. Foxcroft, Klára Pyšková, Martin Hejda

Data type: docx

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Supplementary material 2

Direct ordination (CCA) plot showing the overall differences in the distribution of aliens between the first sampling in 2019–2020 and resampling in 2024 (p = 0.002)

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Data type: docx

Explanation note: The plot shows that some aliens, like *Amaranthus standleyanus*, were more frequent in 2019–2020, while others, like *Conyza bonariensis*, were more frequent in 2024. AcanHisp = *Acanthospermum hispidum*, AchrAspr = *Achyranthes aspera*, AltPung = *Althernanthera pungens*, AmarStan = *Amaranthus standleyanus*, ArgmOchr = *Argemone ochroleuca*, BidnBipn = *Bidens bipinnata*, BidnBitr = *B. biternata*, BoerDiff = *Boerhavia diffusa*, ConzBonr = *Conyza bonariensis*, DatrInox = *Datura inoxia*, GompCels = *Gomphrena celosioides*, ChnAlbAg = *Chenopodium album* agg., MalvCorm = *Malvastrum coromandelianum*, MollNud = *Mollugo nudicaulis*, OpunFics = *Opuntia ficus-indica*, OpunStrc = *Opuntia stricta*, PartHyst = *Parthenium hysterophorus*, PortOler = *Portulacca oleracea*, SchkPinn = *Schkuhria pinnata*, SennSept = *Senna septentrionalis*, SesbBisp = *Sesbania bispinosa*, TridProc = *Tridax procumbens*, XantStrm = *Xanthium strumarium*, VerbEnce = *Verbesina encelioides*, ZinnPerv = *Zinnia peruviana*.

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